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EVIDENCE FOR THE HYBRID ORIGIN OF SCIRPUS PECKII

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On the basis of current morphological, cytological, and ecological studies by the author, the sedge *Scirpus peckii* Britt. appears very likely to be a hybrid between *Scirpus atrovirens* Willd. of section Taphrogeton, and either *Scirpus atrocinctus* Fern. or *Scirpus pedicellatus* Fern. of section Trichophorum. Although *S. peckii* has had a rather complicated history according to the taxonomic literature (Brainerd, 1901), there has been little question in the past about regarding it as a distinctive species. Fernald stated (1900) that, "It is a very handsome and unique plant, not closely related to any described species." It is paradoxical that he also described one of the probable parents of *S. peckii* in the same paper. Fernald (1950) considered *S. peckii* to belong to still another section than those already mentioned, section Androcoma, while admitting (1900) that it had some characteristics of section Trichophorum.

MORPHOLOGICAL EVIDENCE

In order to discuss these plants in detail, I prefer to use comparative descriptive terms rather than quantitative terms. It should be borne in mind that these comparative terms only apply to *S. atrovirens*, *S. atrocinctus*, *S. pedicellatus*, and *S. peckii*.

Scirpus atrovirens, one of the putative parents, produces culms from an underground rhizome with relatively long internodes (Plowman, 1906). The leaves, involucral bracts, and scales have a comparatively low length/width ratio. The values for the bracts are expressed as quotients

in table I. The scales have a conspicuous mucronate tip and are arranged in a steep spiral on the spikelet axis. The lateral rays of the inflorescence branch at relatively divergent, sometimes obtuse angles from the main rays. Bulblets often occur where the rays branch. The spikelets are arranged in compact glomerules, and all the flowers of the spikelet mature at about the same time. After the flowers mature, the spikelet ceases to grow. Hence, flowering and spikelet growth occur during a relatively short span of time. The flowers in the lower part of the spikelet generally have two stamens, although sometimes there are three. Toward the top of the spikelet, the flowers lack stamens. The perianth bristles are short and inconspicuous, and have downward protrusions called barbs.

Scirpus atrocinctus and *S. pedicellatus*, the other probable parents of *S. peckii*, are members of the *Scirpus cyperinus* (L.) Kunth complex. The plants of this complex, along with *Scirpus longii* Fern., are commonly called woolgrasses. Except for *S. longii*, I think it is better to regard these woolgrass types as conspecific and only varietally distinct. However I will treat them in the traditional manner for convenience in this paper. In New York and Vermont, *S. atrocinctus* usually occurs in the uplands, while *S. pedicellatus* usually occurs in stream and river valleys. Morphologically the two types are very similar; they differ mainly in color and size, *S. atrocinctus* is a slender plant with black scales, and *S. pedicellatus* is a robust plant with brown scales. Both types flower approximately at the same time as *S. atrovirens*, while *S. cyperinus (sensu stricto)* flowers later in the summer.

These two woolgrass types have underground rhizomes with short internodes (Plowman, 1906) and form large tussocks. The leaves, involucral bracts, and scales have a comparatively high length/width ratio. Unlike *S. atrovirens*, the scales do not have a conspicuous mucronate tip and they are arranged in a shallow spiral on the spikelet axis. The lateral rays branch at acute angles from the main rays and only rarely do bulblets occur where the rays branch. The spikelets are solitary and the flowers mature

gradually from the base to the tip of the spikelet. The tip continues to grow over a relatively long span of time. The flowers in the lower part of the spikelet generally have 1 or 2 stamens, but higher in the spikelet, most flowers lack stamens. However, in contrast to *S. atrovirens*, there are a few bisexual flowers scattered throughout the upper part of the spikelet. The perianth bristles are long, conspicuous, and without barbs.

The suggested hybrid, *S. peckii*, produces culms in tussocks similar to *S. atrocinctus* and *S. pedicellatus*. The leaves, involucral bracts, and scales have a length/width ratio which is intermediate between *S. atrovirens* and the woolgrasses. The scales do not have a conspicuous mucronate tip, and are arranged in a spiral which is intermediate between

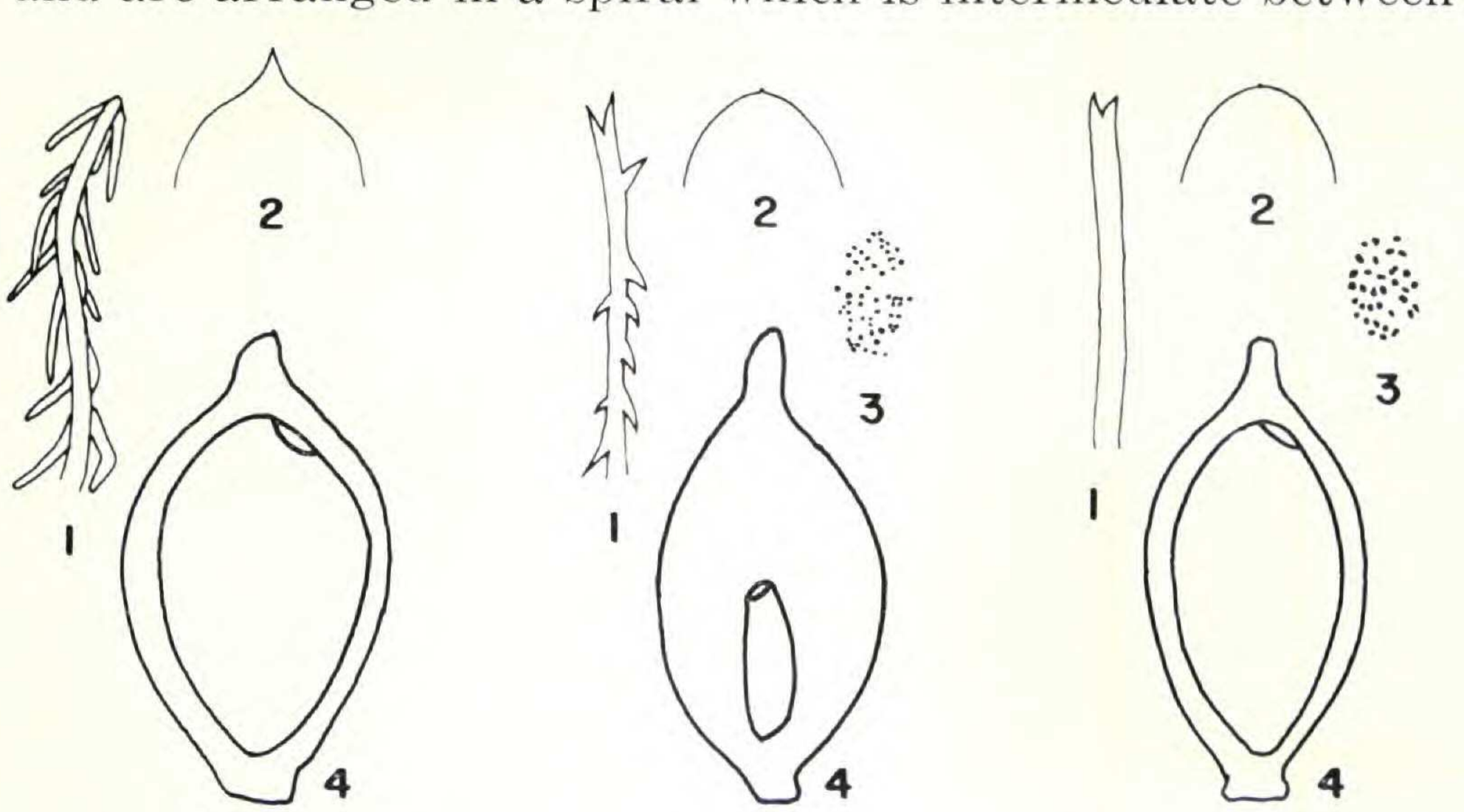

FIG. I. 1. Perianth bristles, x 47 2. Scale tips, x 12 3. Meiotic chromosomes, polar views, metaphase I, x 455 4. Fruits and inclosed seeds, x 34.5.

the steep spiral of *S. atrovirens* and the shallow spiral of the woolgrasses. The lateral rays branch at angles which are intermediate between those of the probable parents. As in *S. atrovirens*, bulblets often occur where the rays branch. The spikelets may be solitary or may occur in small glomerules. At first, the spikelet appears to mature in the same manner as *S. atrovirens*, when about 25 flowers mature at about the same time. However, in contrast to *S. atrovirens*, the tip of the spikelet does not cease to grow, but continues

on to form another tier of flowers. The flowers in the lower part of each tier have two, or occasionally three stamens, and toward the top of each tier, the flowers lack stamens. In this respect, each tier shows a close resemblance to the entire spikelet of *S. atrovirens*. The perianth bristles are about twice as long as those of *S. atrovirens*. Like *S. atrovirens*, the bristles bear barbs, but they are not as long nor are they always protruding downward.

Scirpus peckii also appears to be intermediate between *S. atrovirens* and the woolgrasses on the basis of anther length, style length, and fruit length. However, the differences are minute, and my initial measurements are not complete enough to demonstrate this convincingly.

ECOLOGICAL EVIDENCE

From my observations of *S. peckii* in eleven localities in

TABLE I. A comparison of some characteristics of *Scirpus atrovirens*, *S. peckii*, *S. atrocinctus*, and *S. pedicellatus*.[1]

Character	*S. atrovirens*	*S. peckii*	*S. atrocinctus* *S. pedicellatus*
Growth form	Cespitose, but not tussock-forming	Tussocks	Tussocks
Color at base of lowest involucral bract	Green	Black or brown	Black or brown
Length divided by the width of the lowest involucral bract	16-30	32-53	43-87
Scale length	1.3-1.7 mm.	1.3-1.7 mm.	1.5-2.0 mm.
Scale tip	Mucronate	Mucronulate	Mucronulate
Spikelet arrangement	Glomerate	Solitary to sub-glomerate	Solitary
Flower maturation throughout the spikelet	Almost simultaneously	Gradually in tiers	Gradually
Bristle length	0.7-1.1 mm.	1.6-2.0 mm.	4.5-6.0 mm.
Bristle margin	Strongly barbed	Moderately barbed	Not barbed
Stamen number/ flower*	0, 2, (1), (3)	2, 0, 1, (3)	0, 1, 2

*arranged in order of their frequency of occurrence; parentheses indicate that the number is rarely observed.

[1]The measurements included in this table came from 10 plants of *S. atrovirens*, 15 plants of *S. peckii*, and 15 woolgrass plants.

Vermont and New York, the following pattern appeared: *S. peckii* is widely distributed in these states, but rarely forms large populations; often only 1 to 5 tussocks are found in a particular locality. Further evidence pertaining to this distribution pattern has been provided by Ezra Brainerd (1901). He stated in regard to *S. peckii*, "In a drive of over seventy miles I found single plants of two or three culms each in six stations miles apart." Such an occurrence is unique among the leafy species of *Scirpus* which usually form sizeable populations. In the localities where I observed *S. peckii*, it was always associated with *S. atrocinctus* or *S. pedicellatus*, and, in all but two localities, *S. atrovirens* was also present. Furthermore, there was a morphological correlation between *S. peckii* and the woolgrass type in each locality. In localities where *S. atrocinctus* was the only woolgrass type, plants of *S. peckii* were slender, while in localities where *S. pedicellatus* was the woolgrass type, plants of *S. peckii* were more robust. In one locality, where both woolgrass types were present, both forms of *S. peckii*, the slender and the robust, were present. I think that the unique distribution pattern, and the morphological correlation of *S. peckii* with the associated members of the woolgrass group, give strong additional support for the hybrid origin of this species.

INDICATORS OF HYBRID STERILITY

Further evidence of the hybrid nature of *S. peckii* is provided by its pollen grains, chromosomes, and fruits. Almost all the pollen grains of *S. peckii* which I have observed, have highly distorted walls and their contents do not stain with aceto-carmine. They are in striking contrast to those observed from woolgrasses, which usually have undistorted walls and their contents readily stain with aceto-carmine. I have only been able to make an approximate determination of the chromosome number of *S. peckii*. There appear to be about 60 chromosomes in pollen mother cells undergoing meiosis. This number is approximately the sum of the hypothetical parents. *S. atrocinctus* has a haploid number of 34 and *S. atrovirens* has a haploid number of 25-30 (Hicks, 1928). The chromosome number of *S. pedicellatus* has not yet been determined. Also the units at meiotic metaphase in

S. peckii are smaller in size than those of *S. atrocinctus*. Because of their higher number and smaller size, I am inclined to regard the chromosomes of *S. peckii* as univalents. This condition would not be unusual in a hybrid between two fairly unrelated parents. All the fruits of *S. peckii* which I have observed, have lacked mature seeds. These abortive seeds lack mature embryos and an endosperm. Taxonomists have indirectly made use of these seedless fruits as a taxonomic character. Fernald (1950) mentions that the achenes are soft and whitish, and Gleason (1952) mentions that they are very pale. These characteristics are due to the lack of the yellow-brown seed which colors and fills the fruits in other leafy species of *Scirpus*.

CONCLUSIONS

In view of the evidence presented here, I am certain that this widespread northeastern species is really not so "unique" as it first appears. On the contrary, it appears to have achieved its unusual morphological characteristics by combining the characteristics of two well-known and distinctive species. It is very likely a sterile hybrid which arose, and probably is still arising, over the wide geographical area in which the common parents co-exist.

I am somewhat surprised that it has not previously been suggested that *S. peckii* is a hybrid. I think that the reason for this is due to the technical difficulties that we encounter while identifying many species-groups in the Cyperaceae. The search for differentiating characters has to be a critical one in order to make proper species identifications. However, a critical search for similarities has little value for identification purposes. Hence, we naturally tend to overemphasize differences and tend to ignore similarities which may have taxonomic significance. — UNIVERSITY OF MICHIGAN, ANN ARBOR.

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ENVIRONMENTAL VARIATION IN HETEROTHECA SUBAXILLARIS

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A weedy composite, *Heterotheca subaxillaris*, is a prominent member of the dune-grass community on Bogue Barrier, the most southern island of the North Carolina Outer Banks. The plant occurs not only on the open dunes, but also along roadsides and pathways through the shrub zone and into the pine-oak-hickory forest which covers those portions of the island which are most protected from salt spray. The plants on the dunes are low-growing, nearly prostrate forms. The plants in the pine-oak-hickory forest grow erect and to a height of a meter or slightly more. The plants occurring in the shrub zone are intermediate in size between these two extremes.

While most of these plants flower in late summer and early fall, one population (which occurred on both sides of the road adjacent to the bridge which connects the north end of the island with the mainland) was observed in flower all the year-round, some eighty plants being in full bloom on January 19, 1960. Most of the other *Heterotheca* plants on the island were in winter-rosette form at that time. The winter-flowering specimens resembled a plant described by Benke (1928) as *H. subaxillaris* var. *petiolaris*. They were shorter than typical *H. subaxillaris* and more densely pubescent. While a few of the flowering heads were aborted and deformed, most of the capitula were larger (more than a centimeter in diameter) than those of typical *H. subaxillaris*. They flowered on short branches sent up from a persistent rosette, and, as Benke had noted, were very similar in appearance to plants of the closely allied genus *Chrysopsis*.